# ARTICLE
# SWIMMY: Free Software for Teaching Neurophysiology of Neuronal Circuits

**William Grisham, Natalie A. Schottler, and Franklin B. Krasne**
*Department of Psychology, UCLA, Los Angeles, CA 90095-1563.*

To circumvent the many problems in teaching neurophysiology as a "wet lab," we developed SWIMMY, a virtual fish that swims by moving its virtual tail by means of a virtual neural circuit. SWIMMY diminishes the need for expensive equipment, troubleshooting, and manual skills that require practice. Also, SWIMMY effectively replaces live preparations, which some students find objectionable.

Using SWIMMY, students (1) review the basics of neurophysiology, (2) identify the neurons in the circuit, (3) ascertain the neurons' synaptic interconnections, (4) discover which cells generate the motor pattern of swimming, (5) discover how the rhythm is generated, and finally (6) use an animation that corresponds to the activity of the motoneurons to discover the behavioral effects produced by various lesions and explain them in terms of their neural underpinnings. SWIMMY is a genuine inquiry-based exercise producing data that requires individual thought and interpretation. It is neither a cookbook exercise nor a demonstration.

We have used SWIMMY for several terms with great success. SWIMMY solidifies students' understanding of material learned in traditional lecture courses because they must apply the concepts. Student ratings of SWIMMY have been very positive, particularly ratings from students who have also been exposed to a "wet" neurophysiology lab.

Because SWIMMY requires only computers for implementation and makes minimal demands on instructional resources, it provides for a great deal of flexibility. Instructors could use SWIMMY as part of a traditional lab course, as a classroom exercise, in distance learning, or in blended instructional formats (internet with classroom). SWIMMY is now available for free online complete with student and instructor manuals at http://mdcune.psych.ucla.edu.

*Key words: Neurophysiology, simulation, Neuron, neural circuit, central pattern generator, neural oscillators, teaching neuroscience*

Exploring neural circuits as a "wet lab" requires expensive equipment such as amplifiers, oscilloscopes, analog-to-digital converters, electrode manipulators, and vibration-attenuating tables. These resource requirements make such labs impractical at many institutions. Further, wet labs generally require manual skills that need practice, which means that students may have to practice for weeks before they can reliably obtain data. Wet neurophysiology labs often require troubleshooting, which erodes valuable instructional time. Also, some students find experiments on live or reduced preparations ethically objectionable.

To circumvent these problems, we developed SWIMMY. SWIMMY is a virtual fish (Figure 1) that swims by moving its virtual tail by means of a virtual neural circuit.

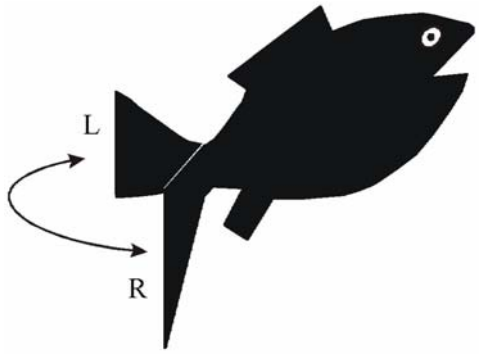


*Figure 1.* Besides including a neural circuit, SWIMMY includes an animation feature that moves its tail based on the activity of its two motor neurons.

SWIMMY offers students the opportunity to approach a conceptually challenging task of scientific discovery and to get practical experience with the basics of neurophysiology —without the impediments of *in vivo* or *in vitro* neurophysiology experiments. SWIMMY is available free online, along with student and instructor manuals, at http://mdcune.psych.ucla.edu.

SWIMMY is written in NEURON (Hines and Carnevale, 2001), a package that allowed us to develop models of neurons and neural networks. Although student modules for examining single cells have been written in NEURON (Meuth et al., 2005; Moore and Stewart, 2007), we believe that SWIMMY is presently unique because it examines ***circuits***.

Rhythmic activity in SWIMMY's motor neurons ultimately derives from a central pattern generator, a central nervous system circuit that generates temporally extended patterns of movement without a need for movement-produced feedback. Rhythmic patterns of activity in neural systems are crucial for such diverse functions as locomotion, respiration, and digestion (Marder and Bucher, 2001). More recently, neural rhythms and central pattern generators that produce them also have been seen as playing roles in sensation, perception, learning, and cognition (Engel et al., 2001; Buzsáki, 2005; Gloveli et al., 2005; Scarpetta and Marinaro, 2005). Students getting a liberal education will benefit from knowing that in centuries past, rhythmic activity has stood as a concrete instance of spontaneous behavior, and understanding its generation in mechanistic terms was

important in establishing that apparent spontaneity does not require non-mechanistic, vitalistic explanations.

Broadly speaking, there are two—not necessarily mutually exclusive—possible mechanisms used by central generators of rhythmic patterns. In one, individual cells might fire repeated, rhythmic bursts of action potentials as the result of their own membrane properties ("single-cell oscillators" or "pacemakers" or "endogenous bursters"). In the other, rhythmic activity might ***emerge from*** circuit and synaptic properties ("circuit oscillators"). In reality, there are a number of forms of each type of oscillator, and in many cases oscillation involves both sorts of mechanism operating cooperatively (Marder and Calabrese, 1996; Marder, 2001). There are several different versions of the SWIMMY program, some of which have a "single-cell oscillator" and some of which have a "circuit oscillator." Identifying different architectures of central pattern generators has been one of neuroscience's greater success stories and has required decades of research. SWIMMY allows students to participate in this enterprise of science in a few weeks.

Exploring SWIMMY and ultimately determining its oscillating mechanism is done in two phases. First students are guided closely through a set of experiments that both teach them to use the program and provide concrete examples of some of the basics of neuron electrophysiology. Secondly, they analyze the circuit mechanisms that generate SWIMMY's rhythmic swimming movements.

## MATERIALS AND METHODS

**Learning to Use NEURON and the Basics of Neurophysiology:** Each aspect of this module builds a foundation for subsequent tasks. Initially, students become familiar with the program by using it to illustrate the basics of neurophysiology. This review will later assist them in attacking the problems of determining the circuit and the mechanism of oscillation. After some rudimentary instructions on using NEURON, students gain further experience in manipulating the program and in dealing with simple circuits (Figure 2, Circuits (a) & (b)) before tackling the main task of analyzing the circuit underlying the swimming behavior.

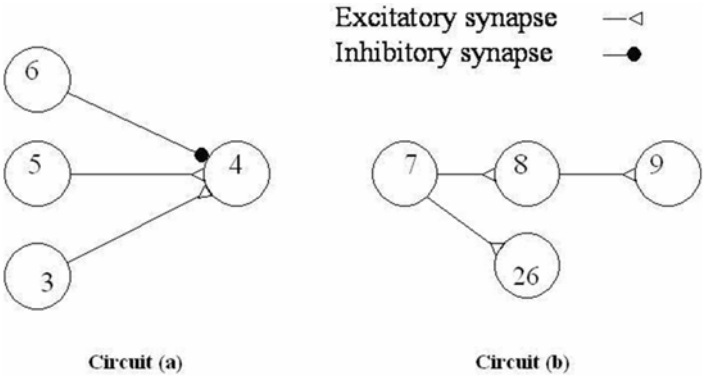


*Figure 2.* Diagrams of simple circuits that students use to familiarize themselves with NEURON and to learn/review basics of neurophysiology.

Specifically, using Circuit (a), students review some of the basics of neural phenomena such as the all-or-none law of action potentials and spatial and temporal summation. Students also investigate the reversal potential of inhibition and see how an IPSP can be inverted to look like an EPSP if the cell is held at a sufficiently negative voltage—a fact they need to know in order to avoid misinterpreting later experiments in which they may hyperpolarize cells to analyze SWIMMY's circuitry. This provides a nice example of the practical importance of understanding some of the finer points of cellular electrophysiology. Students learn the true nature of inhibition—that is that inhibition is not a simple algebraic summation of IPSPs with EPSPs, as many undergraduate textbooks purport, but is substantially due to shunting current through the channels opened by inhibitory neurotransmitter. Further, students learn about short-term synaptic plasticity (in Circuit (a), one of the excitatory synapses depresses and the other facilitates) and come to understand the distinctions between summation and facilitation and between inhibition and depression, concepts that they initially confuse. The synapses in this circuit and others in SWIMMY were borrowed with permission, have been used in published papers (Buonomano, 2005; Karmarkar and Buonomano, 2007), and have both short-term facilitation and depression. (Further details on the neurons and synapses are available at http://mdcune.psych.ucla.edu/modules/swimmy for faculty wishing to set-up a free account.)

Using Circuit (b), students learn about cells having spontaneous activity (Cell 7 is endogenously tonically active and so it continuously makes action potentials). Students learn to appreciate that a cell can be spontaneously active either because it generates activity endogenously (perhaps in collaboration with other cells), or because it is driven by other spontaneously active cells (thus it is a "follower"). Although Cells 8, 9 and 26 also display continuous streams of action potentials, they are followers because they are ultimately driven by Cell 7.

Using Circuit (b), students see a good example of the dogma that correlation does not necessarily imply causation. Temporal correlations are necessary but not sufficient to establish the presence of monosynaptic connections in SWIMMY. In SWIMMY, there is a 1-msec delay between the peak of an action potential and the start of a postsynaptic potential. Both Cell 8 and Cell 26 show a 1-msec delay between the peak of their respective action potentials and the start of the EPSPs in Cell 9. Students are challenged to devise and execute experiments showing that Cell 8 is monosynaptically connected to Cell 9 whereas Cell 26 is not.

**Discovering and Analyzing the Circuit Mediating Swimming Behavior:** The analysis of swimming behavior and its underlying circuit can be done in a great variety of ways. Almost any reasonable approach would probably begin with students identifying which of SWIMMY's 26 neurons are involved in swimming, but this can be done in several ways. One method that is not foolproof but provides a good starting point is to search for neurons

whose activity has a fixed phase relationship to SWIMMY's alternating left-right tail movements. Another is to test whether altering each neuron's activity—by passing currents into it—alters swimming. Once the relevant neurons are discovered, there are several ways in which a student might proceed. Students might systematically determine the connectivity of each neuron of the circuit with every other and continue from there. Alternatively, a less systematic, but also potentially informative approach might be to alter the activities of specific neurons and see what effect this has on the rhythmic activity patterns of the other neurons. For example, if a student found that stopping a particular neuron from firing completely stopped the swimming-correlated activity of all other neurons, then the student would know that that particular neuron was central to the generation of the rhythm.

We generally guide students to divide the problem up into a number of sub-steps as follows: (1) identify the relevant neurons by comparing their pattern of firing to the motor neurons, (2) determine the central pattern generators by doing experiments (most often by blocking or inducing action potentials with current injection), (3) ascertain the neurons' synaptic interconnections both by examining the time relationships between neuron activities and by injecting current to stop or force firing, (4) discover how the rhythm is generated by the central pattern generators, and (5) explain the effects of lesions of various neurons on the behavior of the organism (using the animation depicted in Figure 1, which is directly determined by the activity in the motor neurons).

**(1) Identifying the neurons relevant to the swimming behavior:** Students are given the information that Cells 1 and 2 are the motor neurons. (The pattern of activity of Cells 1 and 2 are shown in Figure 3).

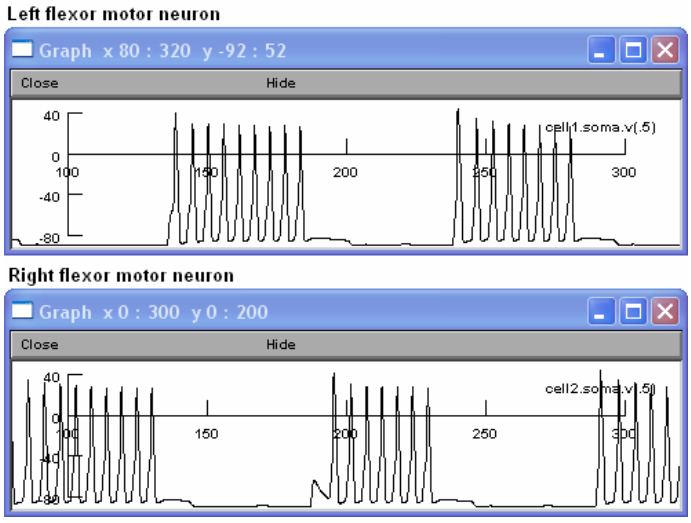


*Figure 3.* Pattern of action potentials in the motoneurons (Cells 1 and 2 in all versions of SWIMMY).

In order to identify neurons that are likely to be involved in the swimming behavior, students are asked to assay the pattern of action potentials in neurons to see if they are reminiscent of that seen in Cells 1 and 2. Cells whose activity occurs in a fixed phase relationship with Cells 1 and 2 are good candidates for being involved in the swimming behavior; cells whose firing pattern bears no relationship to Cells 1 and 2 are not good candidates (Figure 4). (SWIMMY also has some "decoy" neurons that do not participate in any circuit.)

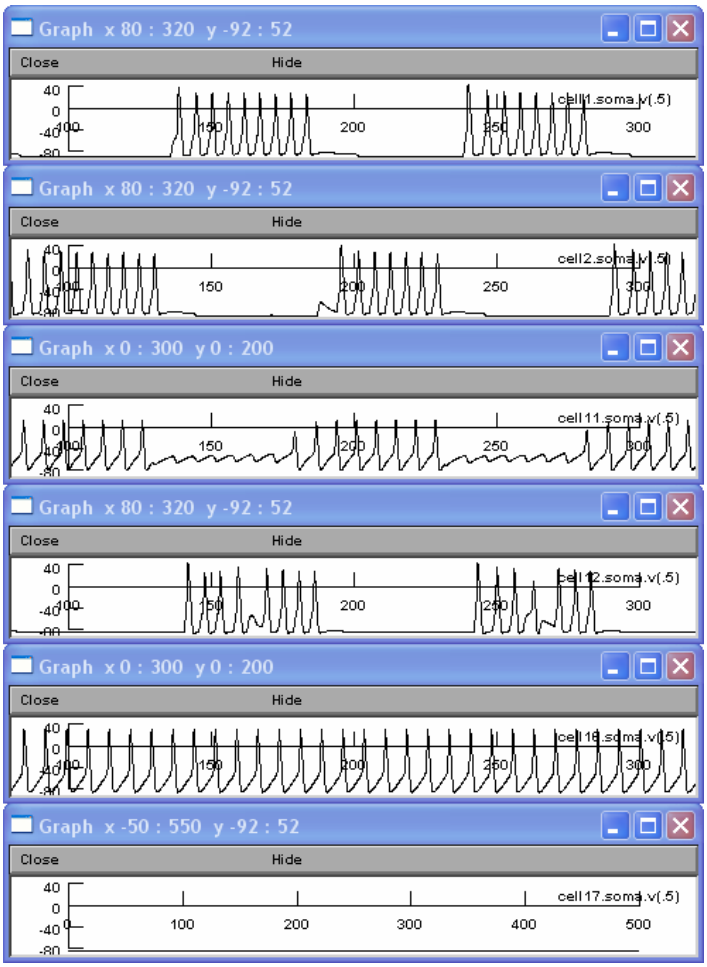


*Figure 4.* Comparing the firing pattern of Cells 1 and 2 (top two graphs) with neurons that are candidates for being part of the swimming behavior circuit (remaining graphs). Cells in the bottom two graphs are not good candidates; cells in the middle two graphs are.

**(2) Determining cells of the oscillating mechanism:** Having identified the neurons involved in swimming, the students are ready to try to figure out how these neurons work together to produce this behavior.

**a) The SWIMMY quiz:** In order to get students thinking about possible mechanisms for the central generation of rhythmic motor patterns, we assign the relevant readings in the student manual and give them a take-home quiz (both the manual and take-home quiz are available online at http://mdcune.psych.ucla.edu). Not only does this quiz help students think about oscillatory mechanisms, the quiz also has hints embedded in it that are clues to the function of neurons in the SWIMMY circuit.

**b) Preparatory interactive discussion:** We have found considerable didactic value in discussing how one

might obtain information about the mechanism of rhythm generation if one can place electrodes in only one cell at a time (the more usual case in neurophysiology). The instructor picks one cell that (unknown to the students) is involved in generating the swimming rhythm and one that is simply a "follower." We begin by trying to get suggestions from the students about how to decide whether a randomly impaled cell is involved in generating the rhythm or is simply driven by other cells. With sufficient hints, the students eventually arrive at the classical test of resetting the phase of rhythmic firing by transiently altering the activity of the recorded cell (by forcing it to fire with depolarizing currents or silencing it with hyperpolarizing ones). We use the Socratic method in such sessions and have the students design and execute an experiment as a group and then discuss how the results should be interpreted. Students respond very well to this sort of interaction; even relatively reticent students willingly participate in the discussion. When students are reluctant to participate in such discussions, the professors leave the room for five minutes with the instruction to discuss amongst themselves while we are gone. This almost invariably produces vigorous discussion and involvement by otherwise silent students (a process on which it is interesting to eavesdrop).

Having established that one of the cells generates its own rhythmic activity and may be part of the oscillating central processing generator (CPG), students learn about the nature of the generation process from further experiments on the CPG cell. We first ask students to suppose that the cell were held in a hyperpolarized state (to prevent it from firing) and then predict the pattern of activity that the cell would reflect if it were part of various oscillating mechanisms. (Oscillating mechanisms are discussed in the student manual available at http://mdcune.psych.ucla.edu). For example, one mechanism posits that alternating bursts of firing are produced by endogenously tonically active cells mutually inhibiting each other via pathways that fatigue with use and recover with rest ("mutually depressing inhibition oscillator"). In such a circuit, one cell fires first and inhibits the other, then the inhibitory synapse depresses and starts to fail, allowing the other cell to fire, which inhibits the first, etc. (Figure 5). Students should realize that if they prevent a cell from firing (by hyperpolarizing it), and if the mechanism of oscillation is a mutually depressing inhibitor, the cell should show a train of IPSPs that either get smaller or possibly even cease, depending on the exact nature of the circuit. Other oscillating mechanisms make other predictions. (We provide three possible oscillating mechanisms in the student manual, from which they can make predictions; examples of these oscillating mechanisms can be seen in Figure 6.)

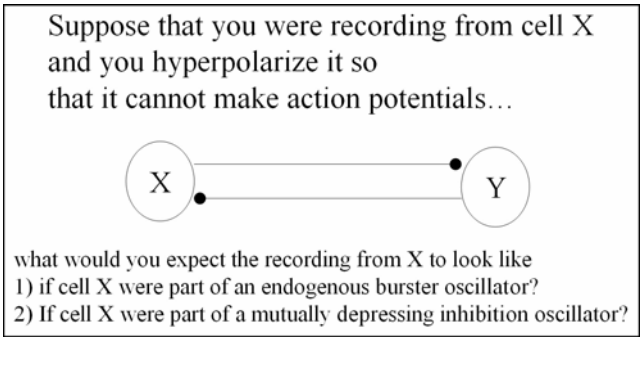


*Figure 5.* Circuit that could be consistent with either a mutually depressing inhibition oscillator or an endogenous burster oscillator. Students are asked to predict what would be recorded if Cell X was hyperpolarized so that it would not make any action potentials but could still receive input from Cell Y, given either oscillator.

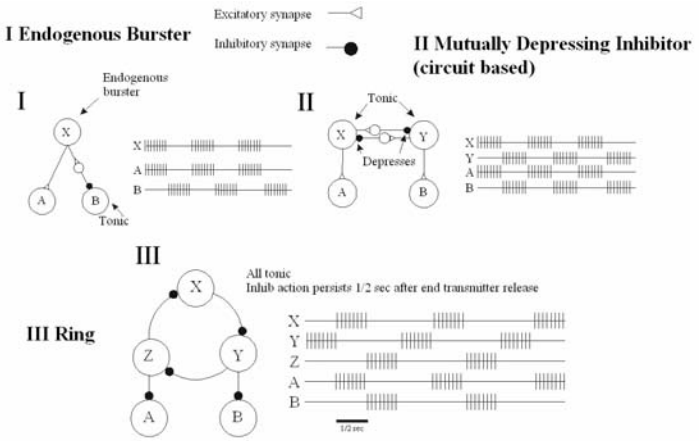


*Figure 6.* Oscillatory mechanisms offered to students as possibilities for their version of SWIMMY. Students must first discern which of these mechanisms is present in their version of SWIMMY and then design and execute definitive experiments to prove their assertion. These schematic diagrams are from the student manual and may or may not match the actual anatomy of SWIMMY so students must decide on the basis of function rather than simply matching the wiring diagrams.

Thus, students see the scientific method in action: creating hypotheses, making predictions from them, testing the predictions, modifying hypotheses if necessary, and eventually coming to an understanding of reality. Also, they see that there is value in deriving predictions from various hypotheses ***before*** doing an experiment rather than just trying things, seeing what happens, and then trying to induce the meaning of the outcome. When we carry out this sort of instruction, sometimes experimental results do not conform exactly to any of the predictions made. This gives us an opportunity to ask whether we need an entirely new theory or whether some minor variant of an existing one could explain the result. These sessions provide a rare opportunity for the students to see and participate in the enterprise in which practicing scientists routinely engage.

**(3) Discovery and proof of monosynaptic connections:** Students must then devise experiments to determine the connections of the neurons in the swimming circuit. When working with Circuit (b) of the initial exercise on basic neurophysiology, students learned that in SWIMMY monosynaptically connected neurons have a 1-msec synaptic delay between the peak of the presynaptic action potential and the start of a post-synaptic potential. They are encouraged to use this fact and to examine the

records that they have already generated for clues to which cells might be monosynaptically connected (Figure 7).

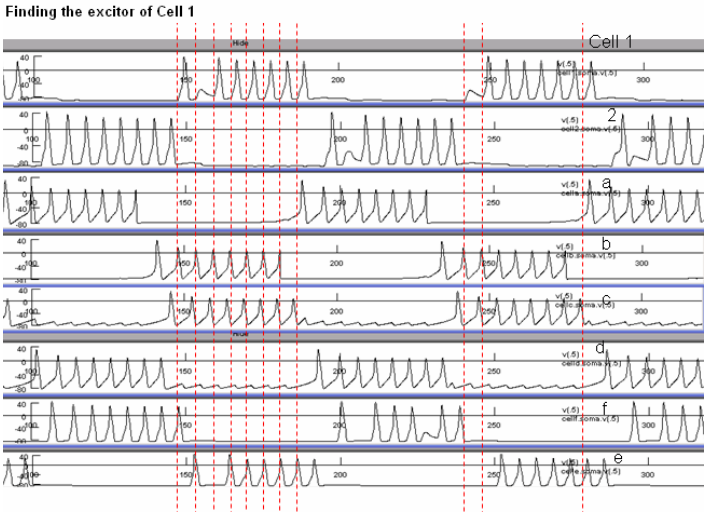


*Figure 7.* Temporal patterns suggest which cells are likely to be monosynaptically connected and which could not possibly be. Only activity in Cell d shows a temporal relationship that would be consistent with it exciting Cell 1.

Excessive delays between spikes in one neuron and synaptic potentials in others can rule out the existence of monosynaptic connections. Also the characteristics of the membrane potential leading up to a spike can give clues as to whether or not they are a product of synaptic activity or are endogenously produced. Nonetheless, a reliable occurrence of a synaptic potential in one cell 1-msec after a spike in another does not necessarily prove that the first cell is monosynaptically connected to the second; often an unknown third cell could monosynaptically drive the first and disynaptically drive the second. Accordingly, we insist that students not only provide evidence of the 1-msec synaptic delay but also provide experimental evidence of the consequent change of activity in postsynaptic potentials when perturbing the activity of the presynaptic cell. This perturbation can be accomplished either by inducing action potentials, by depolarizing the presynaptic cell, or by stopping neurons from firing by hyperpolarizing the presynaptic cell (Figures 8 and 9).

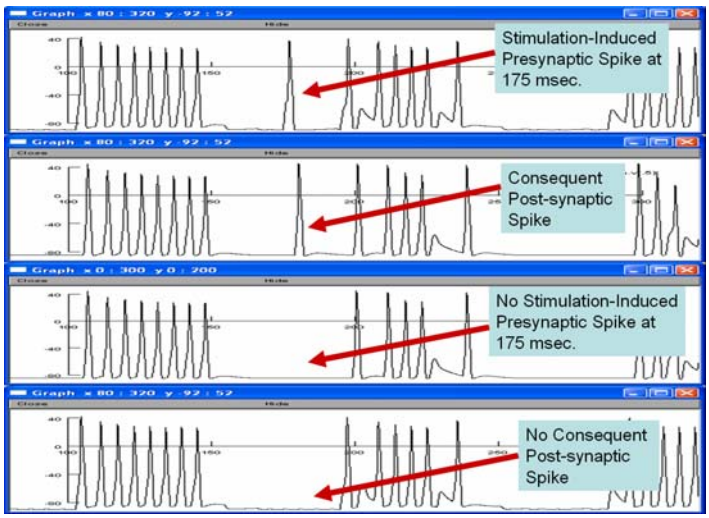


*Figure 8.* Evidence of an excitatory connection. Inducing an anomalous action potential in the presynaptic cell produces an action potential in the postsynaptic cell. One could not necessarily conclude that the connection was direct without illustrating the proper synaptic delay.

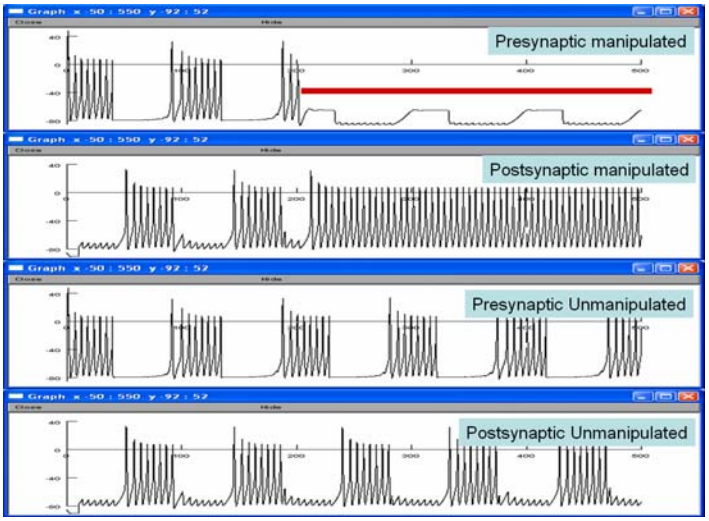


*Figure 9.* Evidence of an inhibitory connection. Hyperpolarizing the presynaptic cell for the duration indicated by the red bar causes the postsynaptic cell to become tonically active. As in Figure 8, although this experiment would show that there was a connection, a monosynaptic connection could only be established if the proper 1-msec delay between the peak of the action potential and the start of an IPSP was also shown.

This aspect of the analysis provides an excellent example of the often-asserted rule that correlation does not prove causation, and we take the opportunity to drive this point home. The experiments establishing monosynaptic connections also provide an excellent arena in which to discuss the need to provide suitable control records when presenting data in lab reports or scientific papers. Students cannot merely present records that show the experimental result alone; they must also show what happened before the presynaptic cell was manipulated.

Once all of the monosynaptic connections are established, students will have a circuit diagram that resembles the connectivity in Figure 10.

**(4) Discover how the rhythm is generated by the central pattern generators:** During the initial exercises reviewing neuron physiology, students became familiar with the notion that some neurons might be crucial to generating a rhythmic activity while others might be rhythmically active only because they receive rhythmic input elsewhere. Students are challenged to make such a distinction in SWIMMY. They are encouraged to begin by seeing what sorts of activity remain in each cell of the circuit when all of its inputs are stopped by hyperpolarization. Notably, individual neurons may be endogenously active without necessarily being involved in the actual generation of the rhythm.

In addition to the methods described in Section (2b)

above, students can ascertain which cells are generating the swimming rhythm by hyperpolarizing cells and seeing whether the alternating pattern of activity is disrupted in at least the entire right or left half of the circuit (Figure 10). If the pattern of activity is disrupted in an *entire* half of the circuit when a given cell is hyperpolarized, that cell was part of the circuit generating the pattern. In contrast, if a follower cell is perturbed, the rhythmic activity in at least some cells in each side of the circuit will be preserved.

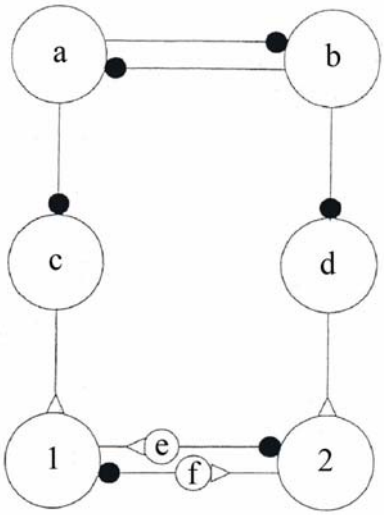


*Figure 10.* Circuit diagram for neurons involved in the swimming behavior. Except for Cells 1 and 2, which are consistent across all versions of SWIMMY, the other cells will have different labels (numbers) in each of the six different versions of SWIMMY.

Students are expected to present experiments with appropriate controls to establish these points. (Specifics of good experiments are discussed in the instructor's manual, which is available at http://mdcune.psych.ucla.edu). Students may find it useful to examine the effects of stopping bilateral pairs of neurons simultaneously.

Some versions of SWIMMY employ single-cell oscillators ("endogenous bursters"), while others employ circuit-based oscillators (Figures 5 and 6). In the former case, endogenous bursters fire bursts of spikes on their own and are kept out of phase with one another via reciprocal inhibitory connections. In the latter case, the cells are each endogenously tonic, and the inhibitory synapses connecting them are subject to use-induced short-term depression—one cell is active until the inhibitory synapse depresses and then the other cell takes over, etc. (Figure 5). Inhibitory ring oscillators are also explained to the students as a foil (Figure 6), but their properties are such that they can be ruled out without specific experiments other than those discussed in Section (2b) above. Students are expected to present experiments with appropriate controls to establish the mechanism of oscillation in their particular SWIMMY. (Specifics of good experiments appear in the instructor's lab manual at http://mdcune.psych.ucla.edu.)

**(5) Explain the effects of lesions of various neurons on the behavior of the organism.** Once students have established the oscillatory mechanism, we ask them to explain the role that each neuron in the circuit plays in forming the final output at a physiological level. Finally, students hyperpolarize or "lesion" one of the motor neurons and then the ipsilateral CPG neuron in turn and compare and contrast these lesion effects on behavior using the animation feature, which directly "reads out" from the motoneurons. Further, they are asked to explain the behavior in terms of their understanding of the functioning of the circuit. As in all phases, we encourage students to present their data in a clear and concise manner so as to easily convince someone else of their conclusions (cf. Tufte, 1990).

## RESULTS

We have used SWIMMY for several terms at UCLA, successfully teaching hundreds of students. SWIMMY supplanted an intensive wet lab exercise in our courses, and we have seen no reason to go back. Digital labs such as SWIMMY have advantages beyond their own merits: 1) They are less expensive to conduct since equipment costs are substantially reduced, 2) Because the equipment consists entirely of computers, it is not specialized and can be used for other purposes, 3) Animal care costs are eliminated, 4) Supplies are virtually unnecessary, 5) Troubleshooting, which erodes instructional time and is not necessarily edifying, is markedly reduced. In terms of instructor time and effort, SWIMMY has allowed us to spend more time focusing on actual instruction and far less time on the mechanics of the preparations.

In response to a survey, most UCLA students felt that they learned a good deal about neurophysiology (Figure 11A) and that using this virtual preparation was superior to using a live animal (Figure 11B).

We probed SWIMMY's efficacy with a preliminary

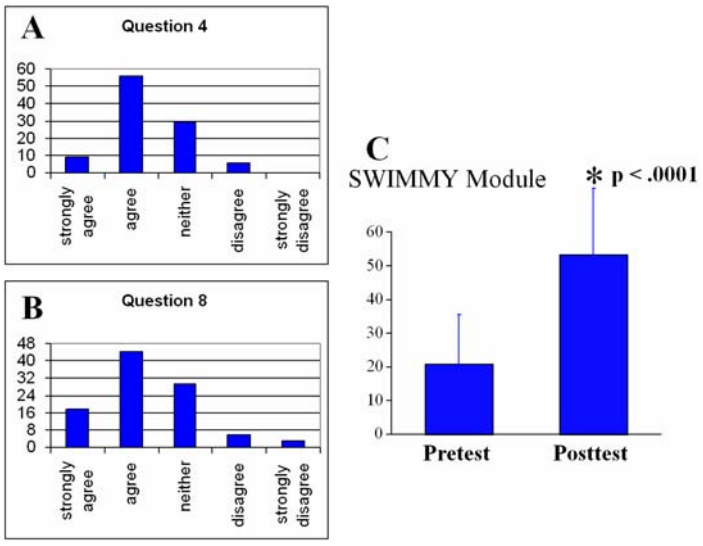


*Figure 11.* A) Question 4: Percent of students agreeing as a function of various scale points in response to a statement that they had learned a good deal about neurophysiology. B) Question 8: Percent of students agreeing that using this virtual preparation was superior to using a live animal. C) Mean percent scores (± SD) Pre- vs. Posttest on assessment measure (n =25).

instrument designed to measure gains by rigorously testing logical and analytic abilities as well as knowledge of basic neurophysiology both before and after the module was presented. The multiple choice instrument included some definitions of concepts taught in SWIMMY (e.g. reversal potentials, Dale's Law) as well as thought problems requiring students to use their understanding of phenomena explored in SWIMMY to deduce the answer. We found that students scored markedly better in the posttest relative to a pretest, $t(23) = 10.378$, $p < .001$ (Figure 11C). We tested the criterion validity of this instrument by correlating pre- and posttest quiz scores with grades on this module. Pretest scores did not correlate significantly with grades ($r(22) = -.273$, $p = .20$), suggesting that grades for this unit did not relate to differential backgrounds that students may have had. Using a slightly larger sample, posttest scores significantly correlated with grades ($r(35) = .341$, $p < .05$), providing some criterion validity for our measure but also suggesting that our instrument could stand some refinement. (The relatively modest correlation could be due to the fact that students are graded partially on the clarity of presentation and soundness of their experiments, which wouldn't be captured by the pre-and-posttest instrument. Further, since the instrument was considerably shorter than the assignment upon which the grades were based, the instrument would be less reliable and subject to more measurement error, which would reduce the correlation. Notably, in the realm of testing, a correlation of .34 isn't bad—it is in the range of the SAT correlation with first year grades.)

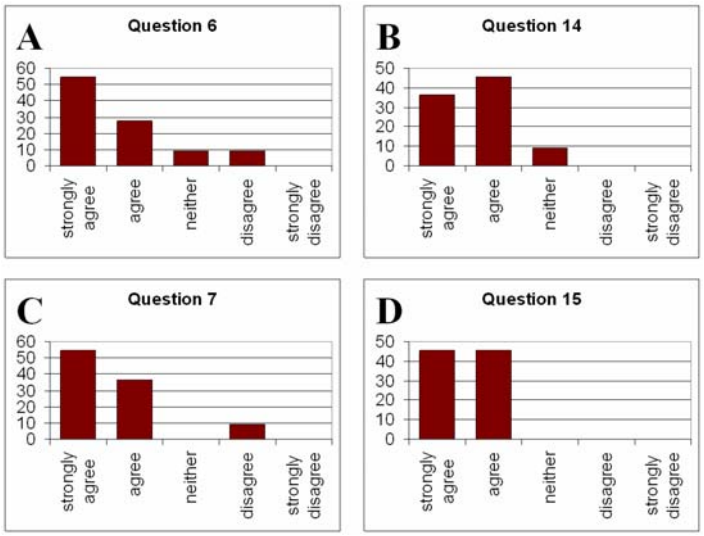


*Figure 12.* Percent of respondents (n = 11) in the Joint Science Department of the Claremont Colleges agreeing as a function of various scale points. Questions were worded as follows: A) Question 6: Using the SWIMMY simulation made learning neurophysiology easier than using the wet-lab preparation. B) Question 14: I felt that the SWIMMY application allowed me to focus more on analysis, interpretation, and synthesis than did the wet-lab preparation. C) Question 7: I learned more electrophysiology from the SWIMMY module because it was less frustrating than using a live preparation. D) Question 15: Using SWIMMY to learn electrophysiology yielded more interpretable results than the wet-lab live preparation.

SWIMMY has also been successfully adopted at a range of other institutions from research institutions to small liberal arts colleges. We were able to measure responses on a survey from students in the Joint Science Department of the Claremont Colleges that had experienced both a wet neurophysiology lab and SWIMMY. These students were very enthusiastically favorable about SWIMMY as a teaching tool. Bar graphs of selected responses to some of these survey questions can be seen in Figure 12.

## DISCUSSION

SWIMMY helps students solidify concepts that they learn in lecture classes and, more importantly, apply these concepts. SWIMMY is not a cookbook exercise; this module produces data requiring individual thought and interpretation. Digital labs like SWIMMY do not sacrifice the inquiry-based nature of the laboratory experience—and even can encourage students to be *more* creative than some wet-lab exercises. Students must compare and contrast the results obtained from their various experiments to create well-reasoned, logical arguments supporting their deductions.

Digital labs such as SWIMMY sidestep the wet-lab emphasis on procedure learning, which can obscure more core areas such as analysis, interpretation, and synthesis. SWIMMY's digital format allows users to go directly to data acquisition, analysis, and interpretation, skipping weeks of tedious and unedifying bench work: students are able to jump right in and collect meaningful data without having to perfect physical procedures. SWIMMY allows laboratory instruction that otherwise would not be practical at the scale of undergraduate laboratories. Students can formulate tractable questions, obtain and analyze data, and interpret the results in a few weeks—replacing the months or years of training and preparation required with a wet lab. Also, student anxiety about procedural errors, which are more reversible in the digital realm, are greatly reduced. Instead, students focus more on bigger questions and on the point of the lesson. In addition, digital labs constrain the numbers and types of procedural errors, making it more likely that the study will yield replicable and interpretable results and allowing students to relate their own data to broader concepts.

SWIMMY has become an integral part of our curriculum, and the evaluation results from the Joint Science Department of the Claremont Colleges show that digital lab experiences can have some clear advantages to wet-lab approaches (Figure 12). When we ran wet labs, students had to work in groups or wait to share equipment, animals, etc. This created the "free rider problem," wherein not all students participated equally, and left dead time while students waited for equipment to become available. With a sufficient number of computers, SWIMMY both allows and calls for each student to be engaged in all aspects of the process throughout all of the instructional time.

SWIMMY provides for considerable flexibility in instructional styles. Above, we describe a systematic

approach to teaching SWIMMY that leads most students to successfully discover the operation of the swimming circuit. Nonetheless, some students may learn more and become much more involved if they try to work things out for themselves. The nature of the guidance that instructors give to students will depend on class size, student backgrounds and abilities, time constraints, etc. Some instructors might consider allowing students to work in groups and collaborate in various ways if formative evaluation is being used and individual efforts are not being evaluated. While this may encourage "free-loading," it also can be educationally valuable to have the students talking with each other about the design and interpretation of experiments. One could even divide students up into rival groups that compete to solve sub-problems first, such as sometimes happens in real-world scientific research.

Because of SWIMMY's digital nature, it can be used in a variety of learning environments, in various modes of delivery, and in varied learning communities. Digital labs can be used in a traditional classroom setting, in a laboratory setting, in blended instruction (internet with classroom), or even in distance learning. We have purposely configured SWIMMY so that it doesn't automatically install itself. This configuration allows flexibility so that students can run SWIMMY on private computers or public computers that may not allow them installation privileges.

SWIMMY's digital nature provides for easy preservation of teaching materials and tools and easy access to these resources for both students and faculty. SWIMMY is part of the Modular Digital Course in Undergraduate Neuroscience Education (MDCUNE), an NSF-funded project to distribute free inquiry-based digital labs via the web. We are delighted to offer this teaching tool to colleagues for free at http://mdcune.psych.ucla.edu.

## REFERENCES

Buonomano DV (2005) A learning rule for the emergence of stable dynamics and timing in recurrent networks. J Neurophysiol 94:2275-2283.

Buzsáki G (2005) Theta rhythm of navigation: Link between path integration and landmark navigation, episodic and semantic memory. Hippocampus 15:827-840.

Engel AK, Fries P, Singer W (2001) Dynamic predictions: oscillations and synchrony in top-down processing. Nat Rev Neurosci 2:704-716.

Gloveli T, Dugladze T, Rotstein HG, Traub RD, Monyer H, Heinemann U, Whittington MA, Kopell NJ (2005) Orthogonal arrangement of rhythm-generating microcircuits in the hippocampus. Proc Natl Acad Sci U S A 102:13295-13300.

Hines ML, Carnevale NT (2001) NEURON: a tool for neuroscientists. Neuroscientist 7:123-135.

Karmarkar UR, Buonomano, DV (2007) Timing in the absence of clocks: Encoding time in neural network states. Neuron 53: 427-438.

Marder E (2001) Moving rhythms. Nature 410:755.

Marder E, Bucher D (2001) Central pattern generators and the control of rhythmic movements. Curr Biol 11:R986-996.

Marder E, Calabrese RL (1996) Principles of rhythmic motor pattern generation. Physiol Rev 76:687-717.

Meuth P, Meuth SG, Jacobi D, Broicher T, Pape HC, Budde T (2005) Get the rhythm: Modeling neuronal activity. J Undergrad Neurosci Ed 4:A1-A11.

Moore JW, Stuart AE (2007) Neurons in action. Sunderland, MA: Sinauer Associates.

Scarpetta S, Marinaro M (2005) A learning rule for place fields in a cortical model: Theta phase precession as a network effect. Hippocampus 15:979-989.

Tufte ER (1990) Envisioning Information. Cheshire, CT: Graphics Press.

Received August 01, 2008; revised November 03, 2008; accepted November 21, 2008.

Acknowledgements: SWIMMY was written by Dr. Franklin Krasne. Development for teaching and preparation for web distribution was done by Dr. William Grisham. Dr. Natalie Schottler contributed substantially to the lab manual. The title for SWIMMY was inspired by a children's book about a little black fish who united all the little fish to protect themselves against the big fish. This charming book by Leo Lionni was a favorite of the daughters of both Drs. Krasne and Grisham, and we would heartily recommend it to anyone buying books for small children. Thanks to Dr. Melissa Coleman for helping procure the survey information from her students at the Claremont Colleges. Thanks to Anne-Marie Schaaf for editing this manuscript. By permission of the developers of NEURON (M. Hines), a version of NEURON is distributed and downloaded along with SWIMMY. Supported by NSF DUE-0717306 to Dr. William Grisham.

Address correspondence to: William Grisham, Ph.D., Psychology Department, UCLA, 1285 Franz Hall, PO Box 951563, Los Angeles, CA 90095-1563 Email: wgrisham@ucla.edu